CLIME

Climate and Lake Impacts in Europe

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Report on changes in algal abundance in relation to weather patterns

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1 Introduction

Phytoplankton has an immediate and strong socio-economic importance for human society as it will influence various human uses of water e.g., as drinking water, tourism, recreation .... Consequently, the possible influence of climate change on phytoplankton development is of immediate concern for human society. A better understanding and prediction of the influence of climate variability on phytoplankton growth patterns based on historical records is one of the main tasks of CLIME's work package 8. Here we report the influence of climate variability on the historic development of phytoplankton growth patterns in the primary and secondary sites of CLIME (Table 1). Using these study sites, we encompass lakes in three different regions, i.e., Western, Central and Northern Europe, and lakes of different setting, morphology, and trophic status.

Table 1. List of lakes in which phytoplankton growth patterns have been analysed in this report

Lake	Country	Surface area	Trophic status
Erken	Sweden	23.7 km^2	Mesotrophic
Esthwaite Water	UK	1 km^2	Eutrophic
Greifensee	Switzerland	8.5 km^2	eutrophic
Constance (Upper Lake Constance)	Austria, Germany, Switzerland	470 km^2	oligo-mesotrophic
Lough Leane	Ireland	19.9 km^2	Mesotrophic
Müggelsee	Germany	7.3 km^2	Hypereutrophic
Mälaren (Ekoln)	Sweden	94.1 km^2	Eutrophic
Mälaren (Galten)	Sweden	61 km^2	Hypereutrophic
Mondsee	Austria	14.2 km^2	Mesotrophic
Peipsi	Estonia	2611 km^2	Mesotrophic
Pilsinger See	Austria	0.134 km^2	oligo-mesotrophic
Pääjärvi	Finland	13.42 km^2	Mesotrophic
Valkea Kotinen	Finland	0.042 km^2	Dystrophic
Võrtsjärv	Estonia	270 km^2	Eutrophic
Windermere	UK	8 km^2	mesotrophic
Lower Zürich	Switzerland	65 km^2	Mesotrophic
Upper Zürich	Switzerland	20 km^2	Mesotrophic

The first part of the report introduces the study lakes. It analyses the main drivers of variability in phytoplankton growth patterns and the response of phytoplankton growth patterns, i.e. biomass and timing events to climate variability in the respective lakes. It also reports and discusses influences other than climate variability on phytoplankton growth patterns, most notably the influence of cultural eu- and oligotrophication. In the second part of the report a comparative analysis of the lakes responses to climate variability is given.

2 Lake specific results

2.1 Lake Constance, Germany, Austria, Switzerland

Lake Constance is a large mono-mictic and deep perialpine lake which was subject to strong eutrophication and oligotrophication in the last century. During eutrophication, maximum phosphorus concentrations during winter mixis rose from 8 $\mu g\ l^{-1}$ in the 1950s to approximately 80 $\mu g\ l^{-1}$ in the 1970s. Since the 1980s total phosphorus concentrations decreased again and dropped to 12 $\mu g\ l^{-1}$ during recent years. The consequences of oligotrophication for Lake Constance has been subject of a number of studies (Bäuerle and Gaedke 1998).

Also, a number of previous studies have shown that Lake Constance and at least its zooplankton community is strongly influenced by climate variability associated with the North Atlantic Oscillation (Straile and Adrian 2000;Straile 2000;Straile, Jochnk, and Rossknecht 2003) Here we analyse the response of phytoplankton growth patterns to the reduction in nutrient loads and to climate variability based on measurements of chl a concentrations from 1980 – 2003 (no measurements available in 1984 and 1985) with a weekly sampling frequency during the vegetation period. In addition we were interested in the effect of the temporal resolution of the analysis. To analyse this we performed our calculations both with the original weekly data as well as with monthly averages of original data.

In respect to the response of chl a to TP concentrations both types of analyses yielded similar results at least during the growing season. Reductions in chla concentrations with oligotrophication, i.e. a positive correlation between chla and TP concentrations, were observed during May and July, i.e. during the timing of the phytoplankton spring and the summer peaks. In

addition significant correlations were observed in the analysis based on monthly averages in March and November. However, the ecological significance of these observations is unclear. Hence, the main response of overall phytoplankton expressed as chla concentrations to oligotrophication of Lake Constance seemed to take place during the periods of the spring and summer phytoplankton peaks.

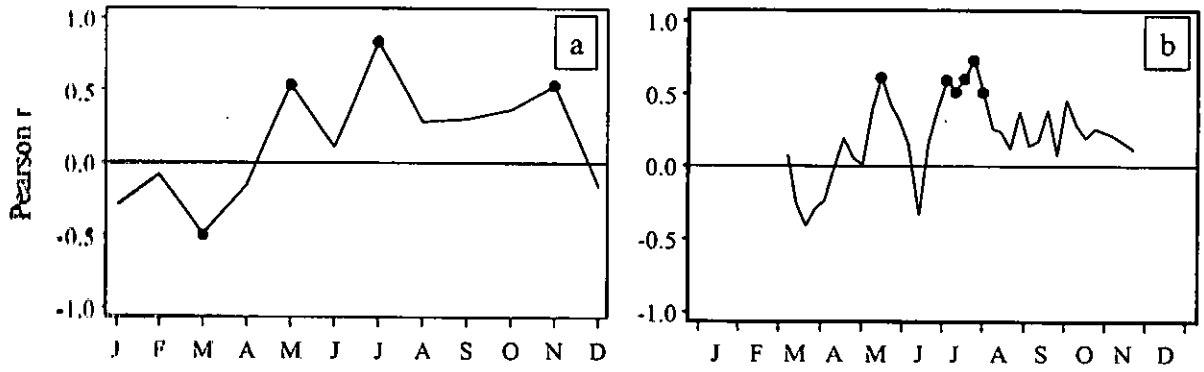

Fig. 1 Seasonal development of the relationship between Lake Constance a) monthly averaged epilimnetic [chla] and b) weekly measurements of [chl a] with [Total Phosphorus] measured during winter mixis. Dots indicate individual correlations significant at $p < 0.05$.

The relationship between chlorophyll concentrations and the NAO index was analysed after time series were linearly detrended. Correlations of monthly chl a averages with the NAO index revealed no significant influence of NAO variability on chl a concentrations (Fig. 2a). Using the weekly series, however, a pattern emerges during summer and autumn (Fig. 2b). During June/July and again in autumn correlations are mostly positive, whereas in-between, i.e. during August/September negative correlations prevail. The reason for this cyclic behaviour remains unclear. Most probably, this results from a predator-prey interaction of algae with *Daphnia*. The latter has been shown to respond very sensitively to NAO variability in Lake Constance (Straile 2000).

In concordance with previous studies (Straile and Adrian 2000;Straile 2000), we found no influence of the NAO on algal dynamics in spring, despite the NAO has an influence on water column stability of Lake Constance in April and May (Straile, Joehnk, and Rossknecht 2003). During these months phytoplankton seems to be controlled at least partially by small herbivores. In contrast, during March physical forcing, i.e., absence of wind induced mixing, which seems to be unrelated to the

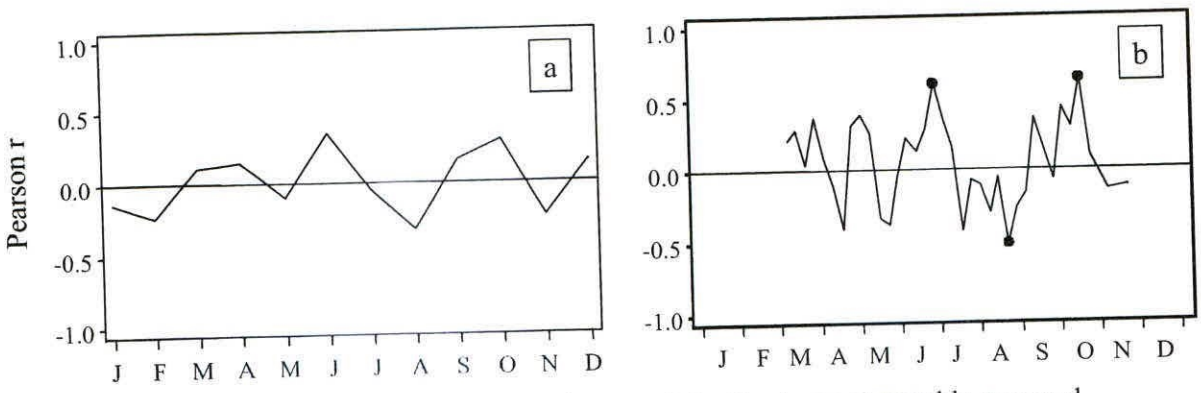

Fig. 2 Seasonal development of the relationship between Lake Constance a) monthly averaged epilimnetic chla concentrations and b) weekly measurements of chl a concentrations with the NAO winter index (Hurrell 1995).Dots indicate individual correlations significant at $p < 0.05$.

NAO is important for the start of the algal bloom (Gaedke, Ollinger, Bäuerle, and Straile 1998). Absence of mixing as indicated by an albeit small temperature gradient was associated with a strong gradient of chl a concentrations with surface [Chl a] more than 3-fold higher in years with a temperature gradient than without a temperature gradient (Fig.3).

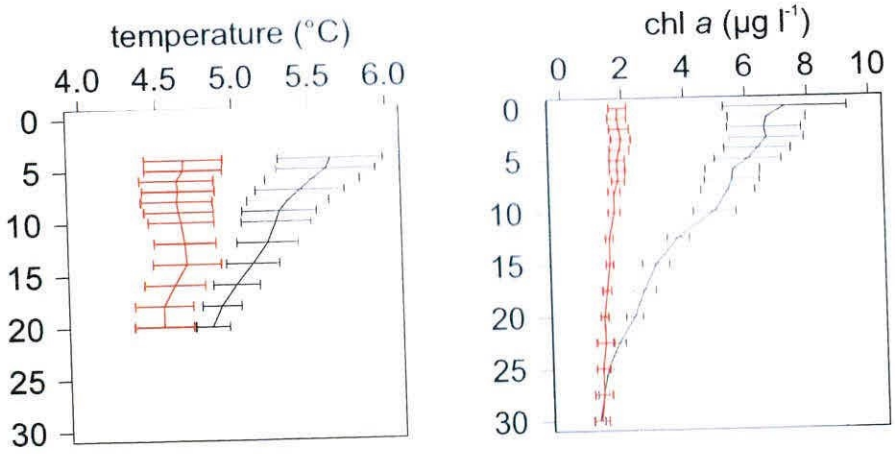

Fig.3 Average March temperature and chlorophyll *a* gradients in years with (black) and without (red) a temperature gradient (= temperature difference between <5m and 15-20m water depth) in March in Lake Constance.

Altogether our studies show that a multitude of factors influence phytoplankton growth patterns in Lake Constance. Reduction of nutrient loads, i.e. oligotrophication is definitely of major importance. In addition, there is also an influence of climate variability, which is however not necessarily associated with the NAO. The influence of the NAO on phytoplankton growth

patterns is most probably an indirect one, mediated by food web interactions with *Daphnia*. Finally, a high temporal resolution, i.e. based on weekly measurements, of the analysis seems to be important to detect these indirect effects of the NAO.

2.2 Lakes Greifen, Zurich and Walen , Switzerland

Phytoplankton data from four lakes (Greifensee, Walensee, Upper Zürichsee and Lower Zürichsee) are available from 1975 to 2000 on a monthly basis (26 years). The lakes are located in the northern perialpine region (at ~420 m a.s.l.). They lie close to one another, in the vicinity of the city of Zurich, and are subjected to approximately the same local weather conditions (Anneville et al. 2004). However, they differ in many other respects. Their surface areas range from 8.5 km^2 to 67 km^2, their maximum depths from 32 m to 150 m, and their trophic states from oligotrophic to very eutrophic.

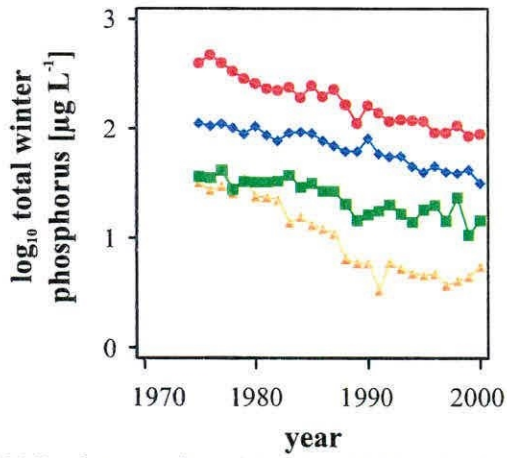

Fig. 4 Time-course (1975 to 2000) of mean winter (D,J,F) total phosphorus concentration in four swiss lakes. Red: Greifensee, blue: Lower Zürichsee, green: Upper Zürichsee, yellow: Walensee.

Greifensee

Greifensee is not only the smallest of the four lakes (surface area 8.5 km^2; max. depth 32 m), but also the most eutrophic. The mean winter total phosphorus concentration ($P_{tot,w}$) from 1975 to 2000 was 202 μgL^{-1}. Greifensee is undergoing strong re-oligotrophication (Bürgi et al. 2003): in the late 1970s, $P_{tot,w}$ ranged between 286 and 472 μgL^{-1}, whereas in the late 1990s it ranged

between 85 and 117 μgL^{-1} (Fig. 4). This decrease in $P_{tot,w}$ is significantly negatively correlated with time ($r = -0.92$, $p < 0.0001$). Phytoplankton biomass showed a strong seasonality, which is typical for eutrophic lakes (Bürgi 1994; Bürgi et al. 2003). Winter values were low (around 1 to 2 mgL^{-1}), but increased 2.5 times from winter to spring, reaching a mean spring peak biomass of ~5 mgL^{-1} in March/April. The spring peak is followed by a pronounced clear-water phase in May/June with values of ~2 mgL^{-1}. After the clear-water phase, a second, hump-shaped, bloom became established, with a peak in July (4 mgL^{-1}). From July to December, biomass decreased continuously. Although $P_{tot,w}$ decreased dramatically during the study period, no significant relationships between the decrease in $P_{tot,w}$ and the phytoplankton biomass were found in winter and spring. Significant negative correlations in June and October indicate a reduction in the magnitude of the clear-water phase (June) and an extension of the late summer bloom (October). No significant correlations with climate variability (e.g., with the winter NAO index, NAO_w) were found.

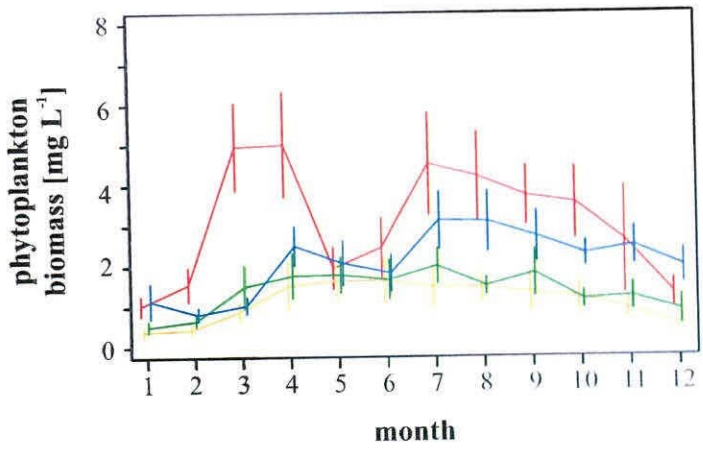

Fig. 5 Mean (1975 to 2000) phytoplankton biomass seasonality in four swiss lakes. Red: Greifensee, blue: Lower Zürichsee, green: Upper Zürichsee, yellow: Walensee.

Walensee

Walensee is the deepest and most oligotrophic of the four lakes (surface area 24.2 km^2; max. depth 151 m; mean $P_{tot,w}$ 13.5 µgL-1). Although very oligotrophic, Walensee underwent a significant re-oligotrophication ($r = -0.91$, $p < 0.0001$) during the study period, with maximum values of $P_{tot,w}$ of ~30 μgL^{-1} in the late 1970s. $P_{tot,w}$ values are currently ~4.5 μgL^{-1}. The seasonal

development of the phytoplankton biomass showed the hump-shaped pattern that is typical of oligotrophic lakes. The maximum biomass (~1.5 mgL^{-1}) occurred on average in May/June. Re-oligotrophication was found to have strongly affected both the absolute phytoplankton biomass and its seasonality (Zimmermann 1999). During the more eutrophic phase, the spring bloom reached values of ~3 mgL^{-1} in March and April, followed by a weakly pronounced clear-water phase, and a weaker second bloom during late summer/autumn with maximum values of ~2.5 mgL^{-1} in October. In the recent, more oligotrophic phase, no clear distinct seasonal patterns were observed, except a weak late summer peak (~1.5 mgL^{-1}) in August. This trend is reflected in the significant positive relationship found between phytoplankton biomass and $P_{tot,w}$ in March, April, May, September, October and November ($p \leq 0.05$). No significant correlations with the winter NAO index were found. However, we found a significant negative correlation of phytoplankton biomass in April and May with air temperatures in April ($r = -0.49$, $p = 0.02$) and May ($r = -0.46$, $p = 0.02$), respectively. We presume that this was probably the result of stronger stratification occurring at higher air temperatures.

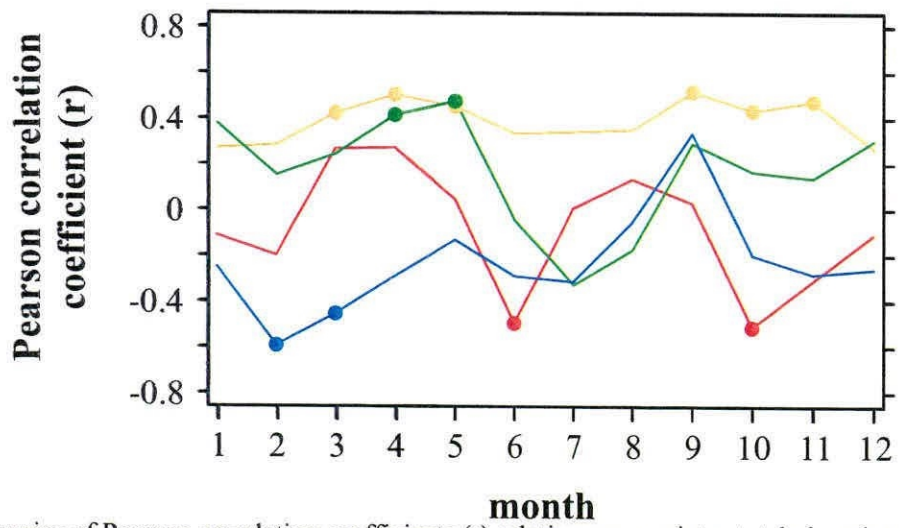

Fig. 6 Time series of Pearson correlation coefficients (r) relating mean winter total phosphorus concentrations to monthly values of the phytoplankton biomass in four swiss lakes. All correlations are for time period 1975 to 2000. Symbols indicate correlations significant at $P \leq 0.05$. Red: Greifensee, blue: lower Zürichsee, green: upper Zürichsee, yellow: Walensee.

Upper Zürichsee

Upper Zürichsee has a surface area of 20 km^2 and a maximum depth of 48 m. With a mean $P_{tot,w}$ concentration of 24.8 μgL^{-1}, this lake is oligotrophic. Upper Zürichsee showed the weakest re-oligotrophication trend ($r = -0.87$, $p < 0.0001$) of all four lakes. $P_{tot,w}$ concentrations ranged between 27.7 and 41.5 μgL^{-1} (mean: 34.8 μgL^{-1}) at the end of the 1970s, whereas at the end of the 1990s, values ranged between 10.7 and 23.4 μgL^{-1} (mean: 17.3 μgL^{-1}). During the more eutrophic period, the seasonal development of the phytoplankton biomass showed a biased hump-shaped pattern, with a peak maximum in April/May (~2.5 mgL^{-1}) and a weak second peak in September. A significant correlation of biomass with trophic state was found for the spring peak (April/May) only, resulting in a reduction of the spring peak (Gammeter and Forster 2002). Summer biomass increased weakly, but not significantly. These two trends have resulted in a more hump-shaped seasonal pattern in recent times (Gammeter and Forster 2002), typical for oligotrophic lakes, with a biomass peak in summer (July), reaching values of ~2.5 mgL^{-1}. A significant negative influence of climate variability (NAO_w) was found in October and November, reinforcing the hump-shaped seasonal pattern. In April, air temperature has a weakly significant negative influence on phytoplankton biomass ($r = -0.36$, $p = 0.075$).

Lower Zürichsee

Lower Zürichsee is the largest of the four lakes (surface area 65 μgL^{-1}; maximum depth 136 m). With mean $P_{tot,w}$ of 71.7 μgL^{-1}, Lower Zürichsee is classified as mesotrophic (Bossard et al. 2001), and ranges between eutrophic Greifensee and oligotrophic Walensee and Upper Zürichsee. Like the other lakes, Lower Zürichsee has undergone a pronounced re-oligotrophication ($r = -0.96$, $p < 0.0001$, Gammeter and Zimmermann 2000). The seasonal development of the phytoplankton biomass showed a pattern intermediate between the patterns shown by the other lakes. The Lower Zürichsee peak biomass in spring and late summer/autumn was higher than those of the oligotrophic lakes, but lower than that of the eutrophic lake. The clear-water phase occurs in May/June, but is much weaker than in Greifensee. Based on the annual means of phytoplankton biomass, no significant decrease could be found during re-oligotrophication (Gammeter and Forster 1997; Zimmermann 1999). However, based on monthly means, re-oligotrophication was found to have had a significant influence on phytoplankton biomass in February and March, with the higher values having occurred in the recent, more mesotrophic

phase. The seasonal pattern did not change between the more eutrophic and the more mesotrophic periods (Zimmermann 1999). A significant negative correlation with the NAO_w index was found in October.

In conclusion, in all four lakes phytoplankton biomass showed at least some significant relationship to re-oligotrophication. In the more oligotrophic Walensee and upper Zürichsee, there is a significant trend back to the hump-shaped seasonality of phytoplankton biomass, which is typical for oligotrophic lakes. In contrast, the more eutrophic ones showed a tendency to a weaker pronounced clear-water phase. However, in all lakes no significant relationships to NAO_w index could be detected, indicating that the oligotrophication process influenced the phytoplankton biomass much more than the winter climate variability.

2.3 Mondsee, Austria

The climate signal controlling spring phenology is seen by time shifts of the spring peak of phytoplankton in Mondsee. In years with a milder winter the spring peak (positive NAO index) is about 39 days earlier, and after colder winter (negative NAO index) about 41 days later than on average (1982-2003). This climatic response is expressed by the negative relationship of the NAO index of January-February to the timing of the spring peak ($r = -0.68$).
Planktothrix agardhii is the most abundant cyanobacteria in deeper strata of the mesotrophic lake Mondsee. Both phosphorus concentrations and the biovolume of *Planktothrix* revealed a decreasing trend for the last 20 years (Dokulil & Teubner, in press). The detrended biovolumes for the cyanobacteria are shown by standardised residuals in figure 1. Warmer spring periods but a colder autumn-winter-period in the same year favors an enhancement of cyanobacteria in Mondsee. We analysed a progression towards 6.5 days longer stratification per decade, demonstrating the climatic responsiveness to the physics of Mondsee. The significant negative relationship between longer periods of stratification and the biovolume of *P. agardhii* suggests that this cyanobacteria in deeper layers is not favoured by warming. The evidence of less cyanobacteria in years of longer stratification is emphasised again by the negative correlation when plotted against the ratio of *P. agardhii* biovolume to total phosphorus concentration ($r = -0.51$).

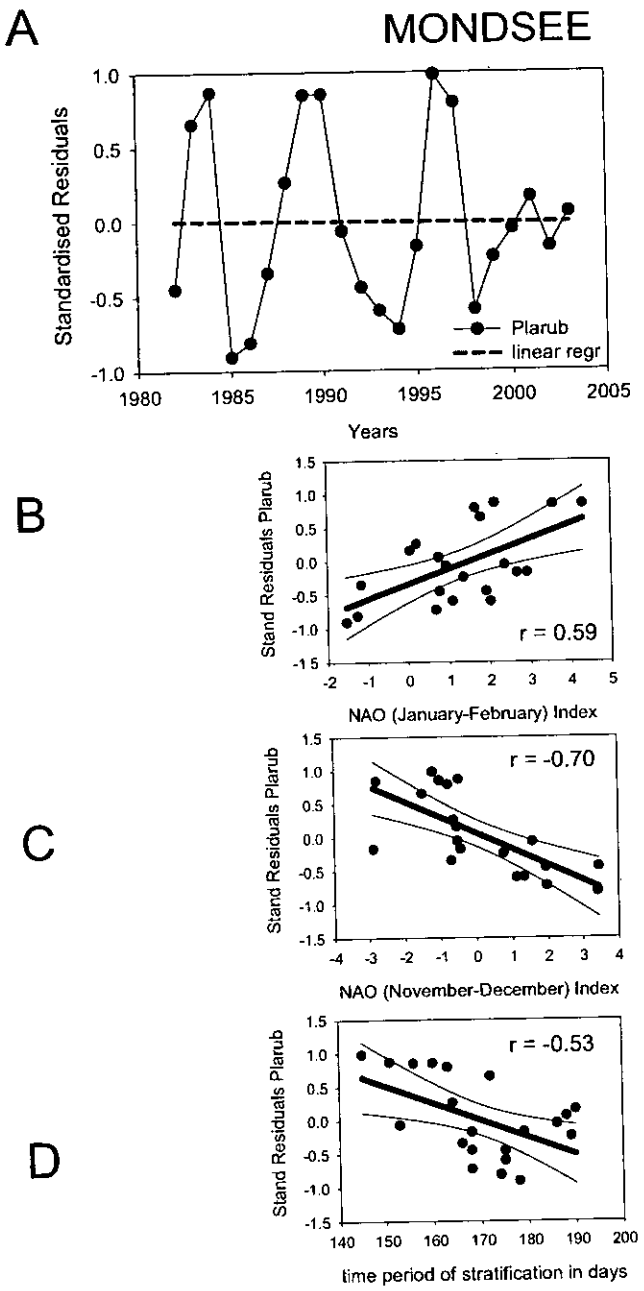

Fig. 7 A: Interannual variation of *Planktothrix rubescens* (Plarub, standardised residuals, effect of detrending is shown by the not existing trend of linear regression) in Mondsee from 1982-2003. B-D: Linear regressions of detrended biovolumes of *Planktothrix rubescens* against the NAO Index for January-February (B) and November-December (C) and the length of the time period of stratification in days (D).

2.4 Müggelsee, Germany

In shallow eutrophic lakes the timing of the spring algal bloom is strongly influenced by the winter conditions – especially the duration of the ice cover or the timing of ice out. In Müggelsee- the timing when maximal algal mass has developed in spring, is currently advancing- associated with a positive phase of the NAO ($r=0.542$, $p<0.01$;

Fig. 8). Between 1979 and 2003 the timing of the spring bloom advanced by 28.5 days. The early timing of the spring bloom was related to changes in the light climate and mixing conditions- advantageous for diatoms -rather than to direct temperature effects.

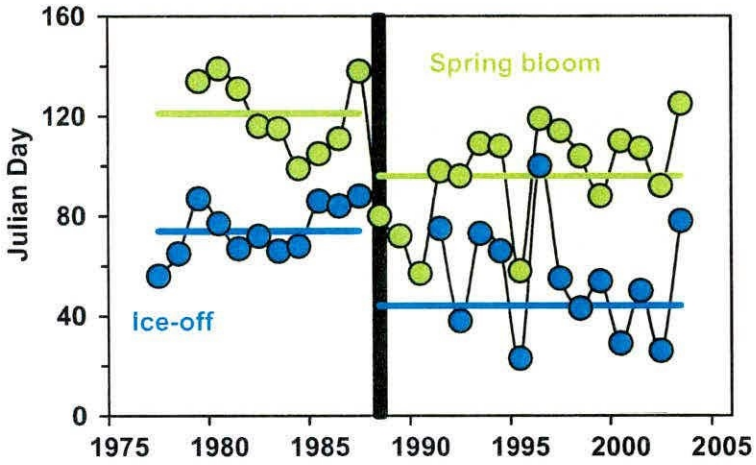

Fig. 8 Timing of spring phytoplankton bloom and ice off date in Müggelsee

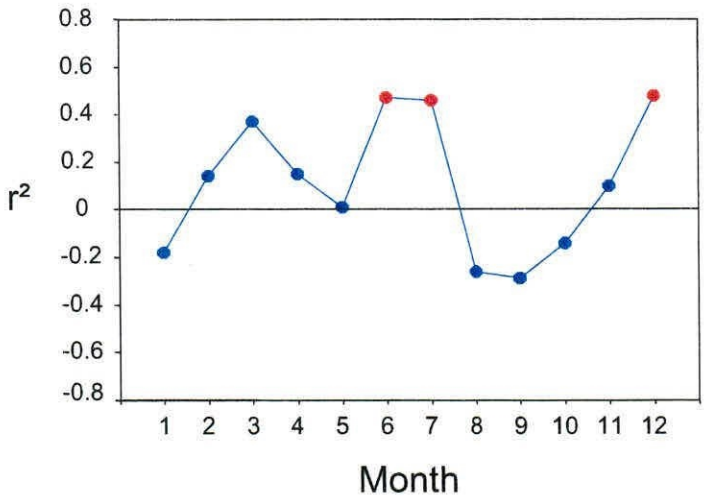

Fig. 9 Correlation of total phytoplankton biomass and NAO index (winter) 1979-2002 in Müggelsee. Significant correlations at 95 % level are marked red.

Overall, total algal mass showed significant correlations with the NAO- winter signal in summer months June and July and unexpectedly in December ($p < 0.05$) (Fig. 9). The expected positive correlation in March was less strong and not significant at the 95 % level.

2.5 Piburger See, Austria

In the last forty years (ca. 1960-2000) the annual development of phytoplankton biovolume in Piburger See has experienced a peculiar evolution, which is strongly related with the changes of the trophic level of the lake. The trophic evolution is, in general, similar to what occurred in many other temperate lakes in the whole Europe, characterised by an eutrophication phase until the late 1970's followed by a slow re-oligotrophication process. However in Piburger See some peculiar aspects are evident as well.

The few historic documents available suggest that in the 50's the lake was still an oligotrophic mountain lake (Psenner *et al.* 1984). Since the early 1960's an eutrophication process started as a consequence of the increase of the nutrient concentrations due to agricultural activities in the lake catchment and to diffuse inputs of domestic waste waters. The eutrophicated condition enhanced the algal production and the aerobic decomposition processes, which induced strong oxygen depletion from 3 m depth down to the bottom of the lake, accompanied by fish death, which was particularly harsh in the winter 1969-70.

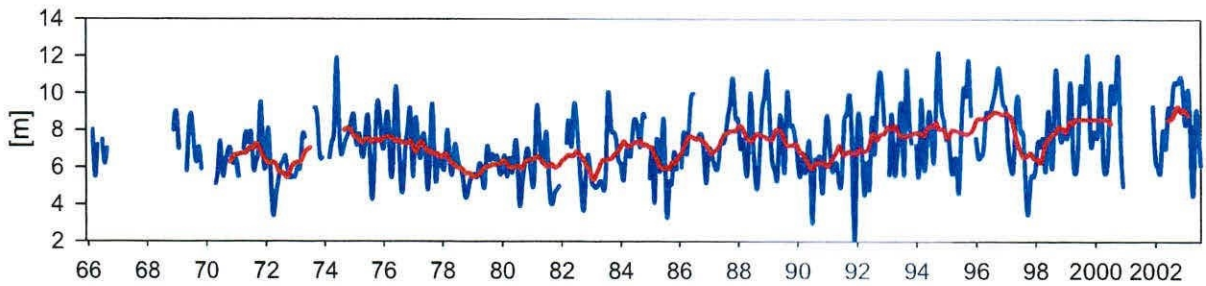

Fig. 10 Secchi depth of Piburger See during the period 1966 – 2002.

In summer 1970 the local authorities decided to start a series of restoration measures, the most important of which were the diversion of waste-waters, the interruption of the use of chemical fertilizers and the installation of an Olszewski tube for the withdrawal of the nutrient rich deep water. The oxygen saturation responded very quickly to the withdrawal of the deep anoxic

waters. However, until the late 1980's no clear effect of the restoration on nutrient level and phytoplankton biovolume could be detected. On the contrary, phytoplankton biovolume, chlorophyll *a* concentrations and Secchi depth increased markedly, reaching extremely high values in spring-summer during until the early-mid 1980's (Fig. 10 and Fig. 11).

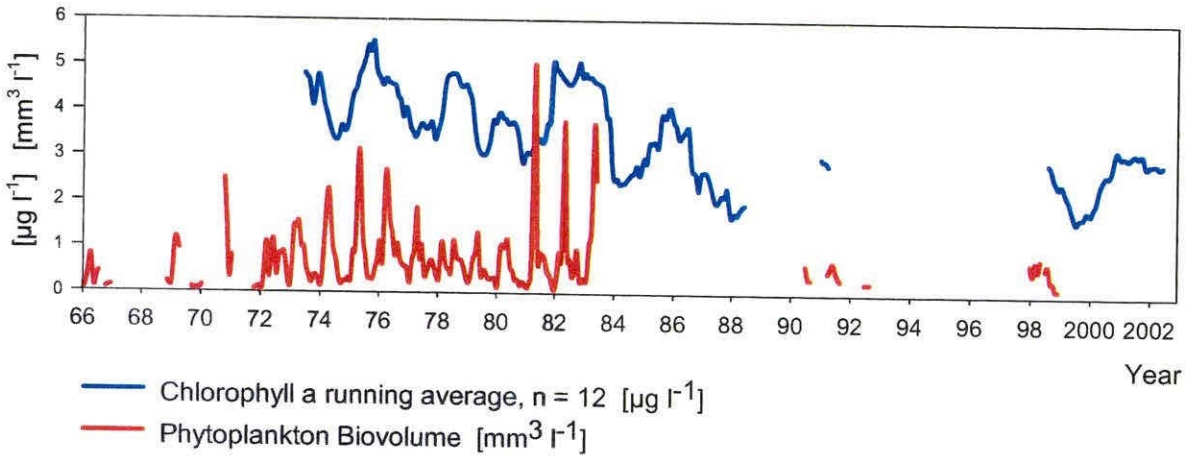

Fig. 11 Chlorophyll a and phytoplankton biovolume of Piburger See during the period 1966-2002.

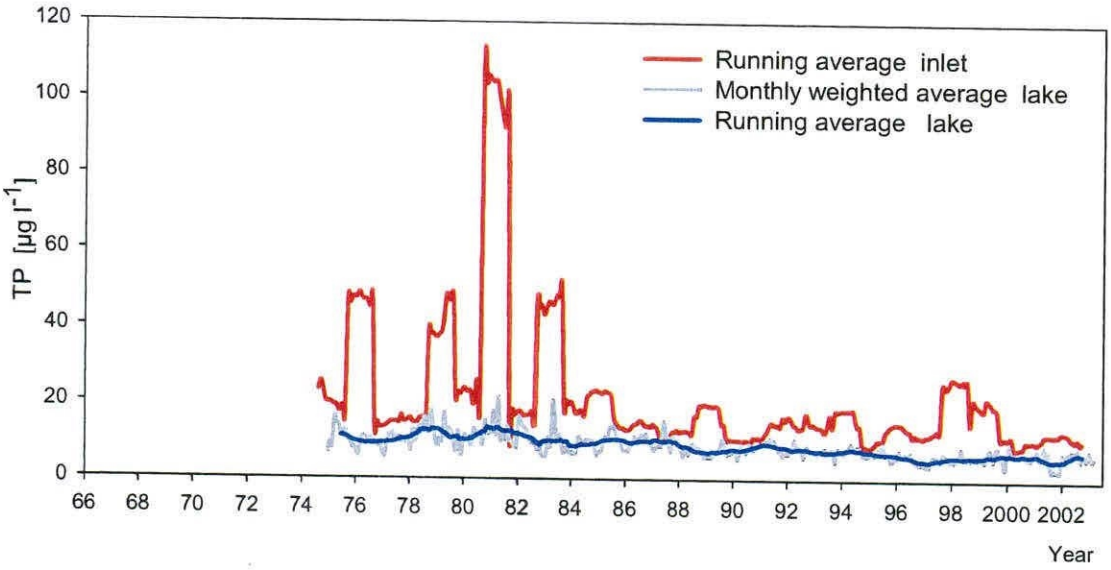

Fig. 12 Total phosphorus concentrations of Piburger See during the period 1966-2002.

The high algal biomass was mainly due to hypolimnetic blooms of the filamentous blue-green algae *Oscillatoria limosa* Agarth, which presented a planktonic growth phase in the deep water

layers from late winter (February) to early summer (June). This phenomenon has been interpreted partially as a response of *Oscillatoria limosa* to the high nutrient (P) inputs from the catchment during the 1980'and partially to the ecological properties of this taxon. In fact particularly high phosphorus s concentrations (up to 130 $\mu g\ l^{-1}$) were recorded in the lake inlet in the early 1980's which are reflected by the higher monthly weighted averages of TP concentrations in the lake.

Moreover, the life cycle of *Oscillatoria limosa*, characterised by a benthonic stage in late-summer and autumn, and its tolerance to low light intensity, which allows the strong growth in the deepest water layers of the lake (Rott 1976), could have primed and prolonged the internal recycling of nutrients after the restoration measures. The internal nutrient recycling has been detected in several lakes during the early re-oligotrophication stages and could be interpreted as responsible for the delay in the recovery of the nutrient concentration in Piburger See as well.

A progressive and regular decrease in the phosphorus concentrations in the main lake inlet and in the lake itself started only in the late 1980 ad was accompanied by a progressive decrease in the chlorophyll a concentrations and phytoplankton biovolume. The decrease in the phytoplankton biomass was principally due to the decrease of the abundance of *Oscillatoria limosa*, which completely disappeared from the plankton of Piburger See since the early 1990's, even though filament mats have been regularly observed on the lake bottom since then.

At present the average chlorophyll concentrations and phytoplankton biovolume remain below 4 $\mu g\ l^{-1}$ and between 0.5 and 1 mm^3l^{-1}, respectively, which are considered as the threshold lines between oligotropic and mesotrophic conditions (Vollenweider & Kerckes, OECD 1982; Rott 1984).

Since the early 1990's even the phytoplankton species composition showed important changes, especially during summer, with an increased abundance of diatoms and coccal blue-green algae (Prader 1993, Tolotti & Thies 2002). At present is not yet clear if these changes are mainly related to the nutrient reduction of if changes in the regional and/or large scale climatic conditions are involved as well. As the increase in the abundance of diatoms became particularly evident since the extremely dry and hot summer 2003, the objective for the near future is to investigate more in detail the relationships between environment conditions and phytoplankton species composition and functionality.

2.6 Esthwaite Water and Lake Windermere

The lakes of the English Lake District have been the subject of intensive study for more than sixty years (Macan, 1970; Talling, 1999). In the early 1960's, Talling and Driver (1963) developed a new method for measuring the chlorophyll *a* content of phytoplankton and this method has since been used to monitor the abundance of algae in all the large lakes. In recent years, the concentration of chlorophyll in most of these lakes has increased due to local discharge of treated sewage effluent and the widespread use of fertilisers. Long-term variations in the weather have also influenced the growth of phytoplankton but these changes are subtle and more difficult to detect. In this report, we use a modelling approach to quantify the impacts of year-to-year variations in the weather on the growth of phytoplankton in two contrasting lakes. Esthwaite Water and Windermere are two of the most intensively studied lakes in the area and are the Primary and Secondary selected for the CLIME project. In each lake, the seasonal variations in the biomass of phytoplankton have been modelled using transformed Gaussian curves and the parameters of the model used to define different aspects of their inter-annual variability. Here we present some Case Studies to illustrate how this approach can be used to quantify the impact of changes in the weather on the duration of the summer growth period for the phytoplankton. Extending the duration of this growing period can have a significant effect on the average biomass of phytoplankton and also lead to an increase in the quantity of oxygen consumed in deep water.

Field Methods - Samples of water and plankton were collected from the lakes by lowering a weighted plastic tube into the water column at a representative central site (Lund & Talling, 1957). The integration depths were for 0-5 m for Esthwaite Water and 0-7 m for the South Basin of Windermere. For most of this period, the samples were collected at weekly intervals but fortnightly sampling was introduced during the winter of 1982 and extended to the whole year in 1992. Vertical variations in water temperature were recorded using a thermistor in the 1950s, a Mackereth oxygen electrode in the 1960s and 70s (Mackereth, 1964) and a Yellow Springs Instrument probe in the 1980s. In the laboratory, the water samples were either analysed immediately for nutrients and chlorophyll content or stored overnight in a cold room at 9°C. Phytoplankton biomass (as chlorophyll *a*) was estimated spectrophotometrically after filtering the samples through a GF/C filter and extracting the pigment with aqueous methanol (Talling & Driver, 1963).

The phytoplankton growth model - The growth of phytoplankton in both lakes followed the 'diacmic' pattern described by Talling (1993) with well-defined maxima in the spring and late summer. The spring maximum is typically dominated by the growth of the diatom *Asterionella* but the species that dominate the summer maximum varied from site-to-site and from year-to-year. The model used to describe the seasonal variations in the concentration of chlorophyll has been described by George and Hurley (2004) and is based on the Gaussian curve, $G(t)$:

$$G(t;\mu,\sigma) = exp\left((t-\mu)^2 / 2\sigma^2\right) / \left(\sigma\sqrt{(2\pi)}\right)$$

where t is the proportion of time that has elapsed from a defined starting date to the current date, that is t = (days from start-date) / 365.
In the model, the concentration of chlorophyll is expressed in logarithmic terms:

$$ln(C(t)) = a + b_1 G(t;\mu_1,\sigma_1) + b_2 G(t;\mu_2,\sigma_2)$$

with the starting date set at 31 December, the start of the 'winter' period. This model generates two chlorophyll maxima when b_1 and b_2 are positive or one chlorophyll maximum when b_2 is zero. The parameters of the model can then be used to characterise the seasonal development of the phytoplankton where:

μ_1 is an index of the timing of the spring growth of phytoplankton (max at $t = \mu_1^{1/p}$)
σ_1 is an index of the duration of the spring growth of phytoplankton.
μ_2 is an index of the timing of the summer growth of phytoplankton (max at $t = \mu_1^{1/p}$)
σ_2 is an index of the duration of the summer growth of phytoplankton.
a is an index of the winter minimum chlorophyll (min ~ exp(a))
b_1 is an index of the magnitude of the spring maximum in relation to the winter minimum (max ~ exp($a + b_1/(\sigma_1\sqrt{(2\pi)})$))
b_2 is an index of the magnitude of the summer maximum in relation to the winter minimum (max ~ exp($a + b_2/(\sigma_2\sqrt{(2\pi)})$))

In this report, we concentrate our attention on the factors that influence the duration of the summer growth of phytoplankton as quantified by the σ_2 (Sigma 2) index. Most of the data analysed was acquired by weekly sampling, but we have included five years where the sampling frequency in summer was reduced to one sample every fortnight.

Fig. 13 shows the result of fitting the Gaussian model to average weekly values of the chlorophyll measurements recorded in the South Basin of Windermere between 1968 and 1997. The results demonstrate that the model provides a very good representation of the average seasonal variations and encapsulate both the timing and amplitude of the two chlorophyll maxima.

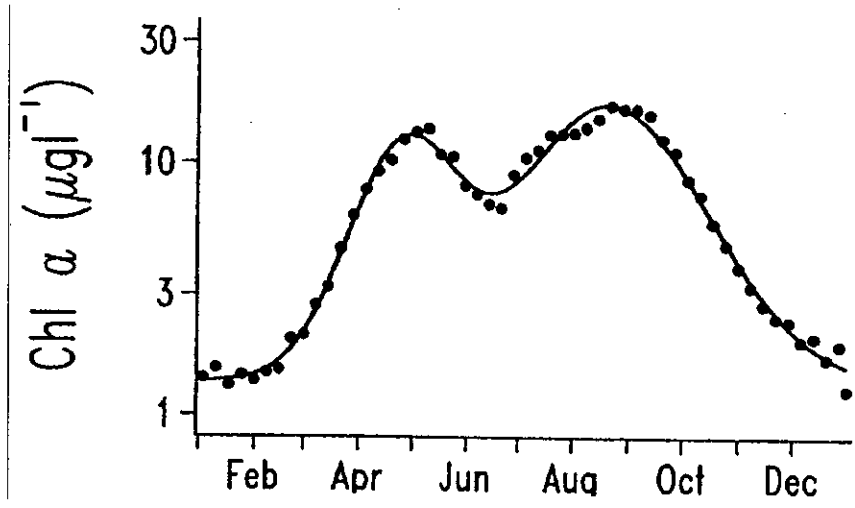

Fig. 13 Fitting the Gaussian model to the average seasonal variation in the concentration of phytoplankton chlorophyll in the South Basin of Windermere. The points are the average of all measurements taken between 1968 and 1997.

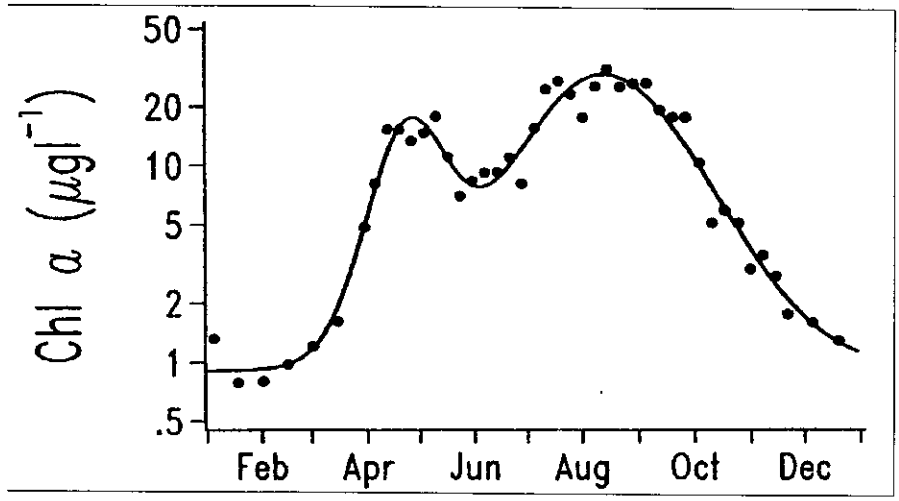

Fig. 14 The observed and modelled concentration of chlorophyll measured in the South Basin of Windermere in 1988. The points show the weekly chlorophyll measurements.

Fig. 14 shows the result of fitting the Gaussian model to the chlorophyll measurements taken in the South Basin of Windermere one particular year (1988). The results confirm that the model can be used to explain a very high proportion of the seasonal variation and resolve key features like the spring growth of phytoplankton and the timing of the clear-water phase.

Fig. 15 shows the results of using the Sigma 2 index to demonstrate the long-term change in the duration of the summer growth period in Esthwaite Water. Despite some pronounced year-to-year variations, there is a clear trend towards a longer growing season with the index increasing from an average of 0.13 in the 1970's to an average of 0.24 in the 1990's. The rate of change is particularly pronounced in the mid 1990's when a number of very warm summers were recorded in the UK.

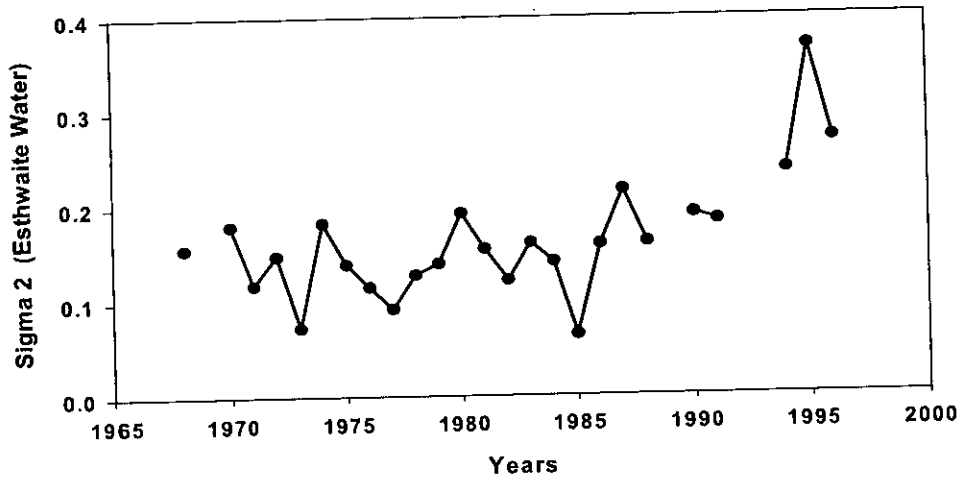

Fig. 15 The year-to-year variations in the Sigma 2 index for Esthwaite Water. This index is a general measure of the length of the growing season. Missing years are cases where the parameter values cannot be reliably estimated.

An analysis of the thermal data acquired during the same period shows that a key factor influencing the duration of the growing season was the heat content of the water column in late summer. Fig. 16a shows the relationship between the length of the growing season and the heat content of the lake in late summer (weeks 31-40). There is a strong positive correlation ($r = 0.56$, $p < 0.05$) between the Sigma 2 parameter and this physical measurement which is an integrated measure of the lakes response to warm summers. Further tests showed that that there were no

significant correlations between the Sigma 2 parameter and any of the individual meteorological variables. There was, however, a weak positive correlation between the Sigma 2 parameter and the average air temperature and a weak negative correlation with the average wind speed recorded during the same late summer period.

(a) (b)

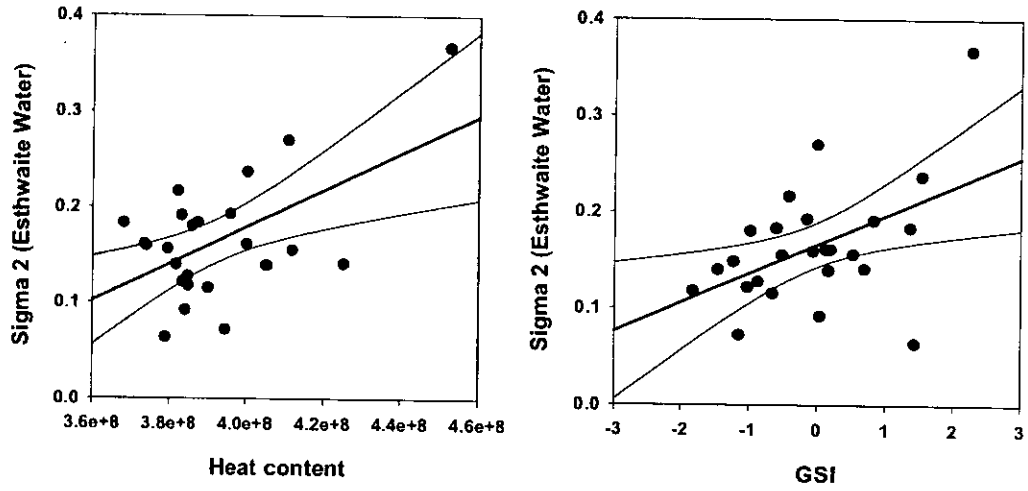

Fig. 16 (a) The relationship between the Sigma 2 parameter and the heat content of the water column in Esthwaite Water in late summer. (b) The relationship between the Sigma 2 parameter and the Gulf Stream Index (GSI).

The only significant correlation recorded with any proxy indicators of climate change was that observed with the latitude of the Gulf Stream (Fig. 16b). Monthly charts showing the position of the north wall of the Gulf Stream have been produced since 1966. An index of this position has also been developed (Taylor and Stephens, 1980) and ranges from strong negative values when the Gulf Stream is positioned towards the south to strong positive values when it is positioned towards the north. The position of the north wall of the Gulf Stream in the Atlantic has previously been shown to influence the movement of pressure systems across the Atlantic and the mixing characteristics of lakes in the English Lake District (George and Taylor, 1995; George, 2000). The results presented here demonstrate that Gulf Stream also effects the duration of the growing season which tends to be longer in years when the Gulf Stream Index is strongly positive.

Previous studies in the English Lake District have quantified the effects of long-term changes in the weather on the average concentration of chlorophyll recorded in particular seasons (George, 2000; George et al.,2004). In the CLIME project, we are using the Gaussian model described here to quantify the year-to-year variations in the seasonal dynamics of the phytoplankton. In this report, we have shown how year-to-year changes in the weather influence the duration of the summer growth period in one of the Windermere lakes. The Gaussian model results from other lakes in the area are currently being collated and will now be used to quantify the changing pattern of phytoplankton growth in a number of contrasting sites.

2.7 Lough Leane, Ireland

The Lakes of Killarney are situated in SW Ireland in County Kerry. L. Leane (52° 05' N, 09° 36' W) is the largest of the three lakes. It has an area of 20 km^2 and a mean depth of 13.4 m. The town of Killarney lies on the shores of the lake. The catchment of 553 km^2 consists of two contrasting components: an area of upland mountain peat and forest which lies to the south and west and drains through the two smaller lakes, Upper Lake and Muckross Lake, into L. Leane and an area to the east of the lake which is mainly agricultural grassland. The lakes are strongly influenced by the temperate oceanic climate that predominates in the region. Annual rainfall is high and can exceed 2000 mm, with over 3000 mm being recorded in some years in the upland areas. Surface water temperatures are seldom greater than 20°C in summer, except during periods of anticyclonic weather. The lakes stratify thermally between June and September. The surface water temperature in winter is typically greater than 4°C, though periods of clear, cold weather may reduce this to near freezing at times. However, ice cover is unknown.

Upper Lake and Muckross Lake have remained oligotrophic in all years since monitoring began in the 1970s. In contrast, L. Leane has undergone several changes in trophic status in recent decades (Fig. 17). The lake was classed as oligotrophic in 1972 and was mesotrophic for most of the period up to the early 1980s. Chlorophyll *a* concentrations then increased and the lake was classified as moderately eutrophic in 1983 and 1984. The change in the trophic state of the lake was linked to increased phosphorus concentrations, primarily from municipal wastes. Following the completion of a new sewage treatment plant for the town of Killarney in 1984, the trophic status of the lake improved and it was classed as oligotrophic in 1990 and 1991 and as

mesotrophic for most of the 1990s. However, in 1997 hypertrophic conditions were recorded in the lake. Strongly eutrophic conditions were again indicated in 1998, with chlorophyll *a* concentrations of 37.8 and 69.5 µg L^{-1} at two of the three sites used for assessment (Fig. 17). This decline in the trophic status of the lake was again linked to increased phosphorus inputs, with diffuse sources thought to contribute the bulk of the increased loading.

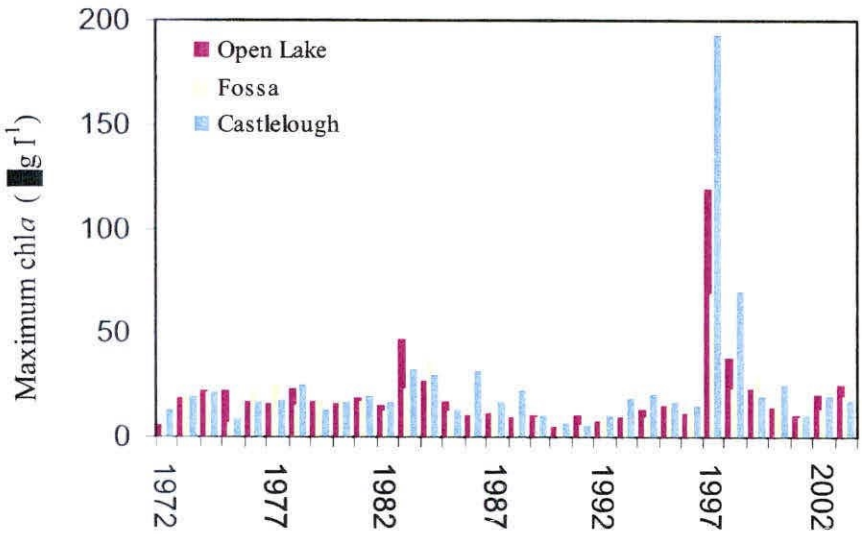

Fig. 17 Maximum chlorophyll a (µg l^{-1}) at three sites in L. Leane: 1972-2003

In the late 1990s the L. Leane catchment monitoring and management programme was initiated. This programme included management measures focused on reducing phosphorus inputs, particularly from diffuse sources. In 1999, the trophic status of the lake improved from strongly eutrophic to moderately eutrophic, while results for 2000 to 2003 indicated a return to mesotrophic conditions.

The impacts of the NAO index on the weather in Co. Kerry was investigated in the REFLECT project using data from Valentia, a synoptic station 50 km west of Killarney, and from Muckross, a lakeshore station at L. Leane (Jennings et al. 2000). The study indicated that mean winter air temperatures in the region were highly influenced by the winter NAO. The effect of the winter NAO on air temperatures persisted to a lesser extent in spring and summer. There was no significant effect by the following autumn. Winter wind speed, relative humidity and cloud

amount were also positively related to the NAO. However, there was no significant relationship between winter rainfall and the NAO. The relationship between solar radiation in the region and the NAO was negative, with higher winter global and diffuse radiation measurements and greater sunshine hours in low NAO years. Winter surface water temperature in L. Leane was also found to have a positive relationship to the NAO.

An inverse relationship was previously reported between mean winter chlorophyll *a* concentrations in L. Leane and the winter NAO index (1976-1992), with highest chlorophyll concentrations being recorded in low NAO years (Jennings et al. 2000). This relationship is still apparent when the data available from 1997 to 2002 is included
Fig. 18) (r = -0.52; p = 0.007; n = 26). No relationship was found between the NAO index and mean or maximum chlorophyll *a* concentrations in other seasons. Phytoplankton growth in winter is dominated by species that are adapted to grow at low temperatures and low light levels (Reynolds 1984; Talling 1993). Loss processes due to washout may also influence chlorophyll concentrations (Reynolds and Lund 1988). A relationship between the winter NAO and winter chlorophyll concentrations has also recently been reported by George et al. (2004) for two small lakes in the English Lake District. This relationship was linked to the influence of the NAO on rainfall and flushing rates. However, the absence of any correlation between the NAO and rainfall in Co. Kerry would indicate that this is not a factor in the observed relationship in L. Leane. In addition there is no relationship between total inflow to L. Leane in the winter period and the NAO.

The lack of any relationship between the NAO and rainfall at this site may reflect variation in the influence of the NAO on weather patterns over Ireland and Britain. Davies et al. (1997) have noted that, in high NAO years, heavier than normal precipitation may be experienced over the northern half of Ireland and Britain, while precipitation may be reduced in the southern half. There were no significant correlations between the meteorological variables that are related to the NAO in County Kerry and mean December-January chlorophyll *a* concentrations in L. Leane with the exception of a correlation with mean air temperature (r = -0.45; p = 0.022). However, this correlation may reflect the influence of the NAO on both variables and does not necessarily indicate that low temperature is part of the driving mechanism in the relationship between the

NAO and chlorophyll *a* in the lake. It is probable that the relationship is due to a combination of more than one meteorological effect and that the NAO index acts as an integrator.

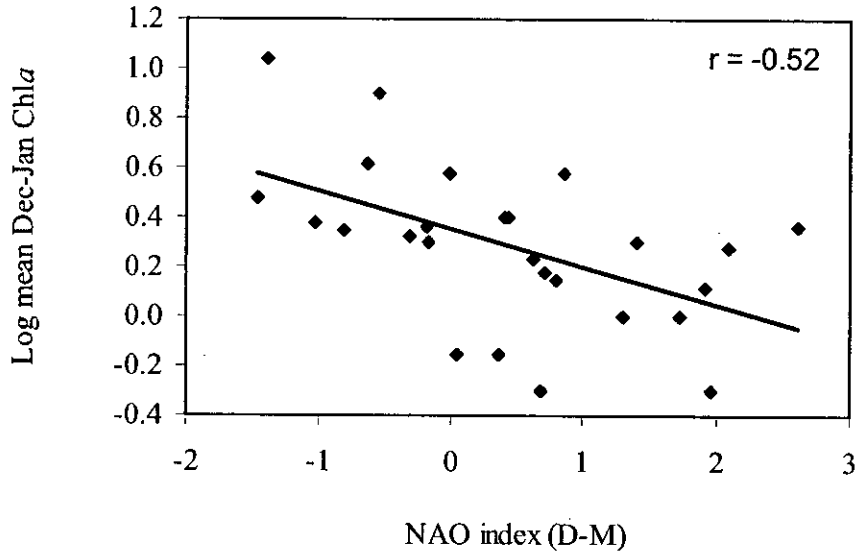

Fig. 18 Mean chlorophyll a concentration (December-January) (log transformed) plotted against the winter NAO index.

In summary, the pattern of summer phytoplankton abundance in L. Leane since the mid-1970s has been highly influenced by changes in the availability of nutrients from the catchment. However, winter chlorophyll *a* concentrations are negatively correlated to the NAO index, with higher chlorophyll *a* concentrations in low NAO years, highlighting the influence of variation in weather at this time of the year. Lower air temperatures with clearer skies and higher light availability characterise the winter weather in low NAO years.

Acknowledgements: We would like to thank Kerry County Council, Aine Ni Shuilleabhain, Pascal Sweeney and the UCD Killarney Valley Project team for use of their data from L. Leane.

2.8 Lake Võrtsjärv, Estonia

Lake Võrtsjärv is a large (270 km^2) shallow (mean depth 2.8m, maximum depth 6m) non-stratified eutrophic lake located in Central Estonia. The mean annual amplitude of water level

fluctuations in this lake is 1.4 m, and the maximum range is 3.2 m. The latter corresponds to 1.4-times difference in the lake area, 2.4-times difference in the mean depth and three-times difference in lake volume (Nõges and Nõges 1999). Thus, changing water level is considered to be the leading factor controlling the ecosystem dynamics of L. Võrtsjärv, first of all through phytoplankton (Nõges et al., 2003).

Climatic and hydrological data series for L. Võrtsjärv basin reach back up to more than 100 years. Air temperature has been measured since 1894, precipitations since 1866, water level since1923, ice-on and ice-off dates since 1924, and water temperature since 1947, water chemistry and phytoplankton biomass and composition since 1960s.

In Estonia the western airflow from the Atlantic during positive NAO remarkably increases air temperature and the amount of precipitation in winter (Tomingas & Jaagus 1999). In high-NAO years the ice cover on L. Võrtsjärv has a shorter duration while the yearly average air temperature and the amount of precipitations in the vicinity of the lake are higher (Fig. 19).

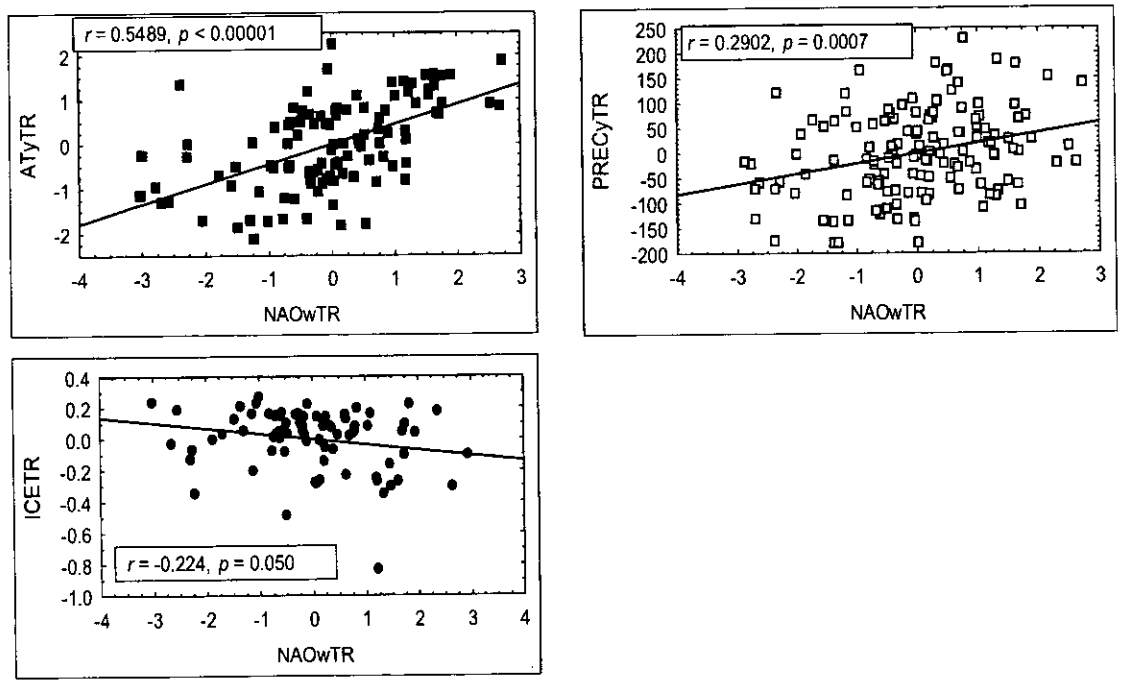

Fig. 19 Correlations of the detrended and transformed time series of annual average amount of precipitation in Estonia (PRECyTR), air temperature in central Estonia (ATyTR), duration of ice cover on Lake Võrtsjärv (ICETR), and the North Atlantic Oscillation Index in winter (NAOwTR)according to Nõges (submitted).

Because of flat landscape and restricted outflow, the increased amount of precipitation in high-NAO years is directly reflected in lake's water level (Fig. 20) that remains high for several months after the flood. In this way the water level in spring determines the water level throughout the whole year.

Phytoplankton biomass is higher in the springs after high-NAO winters but during the other seasons the relation is rather opposite. In summer, and autumn phytoplankton biomass is inversely related with the depth (Fig. 20). This phenomenon has been explained by the reverse relationship between average light intensity and water depth in polymictic water column bringing about light limitation and worse growth conditions to phytoplankton (Nõges and Nõges 1999).

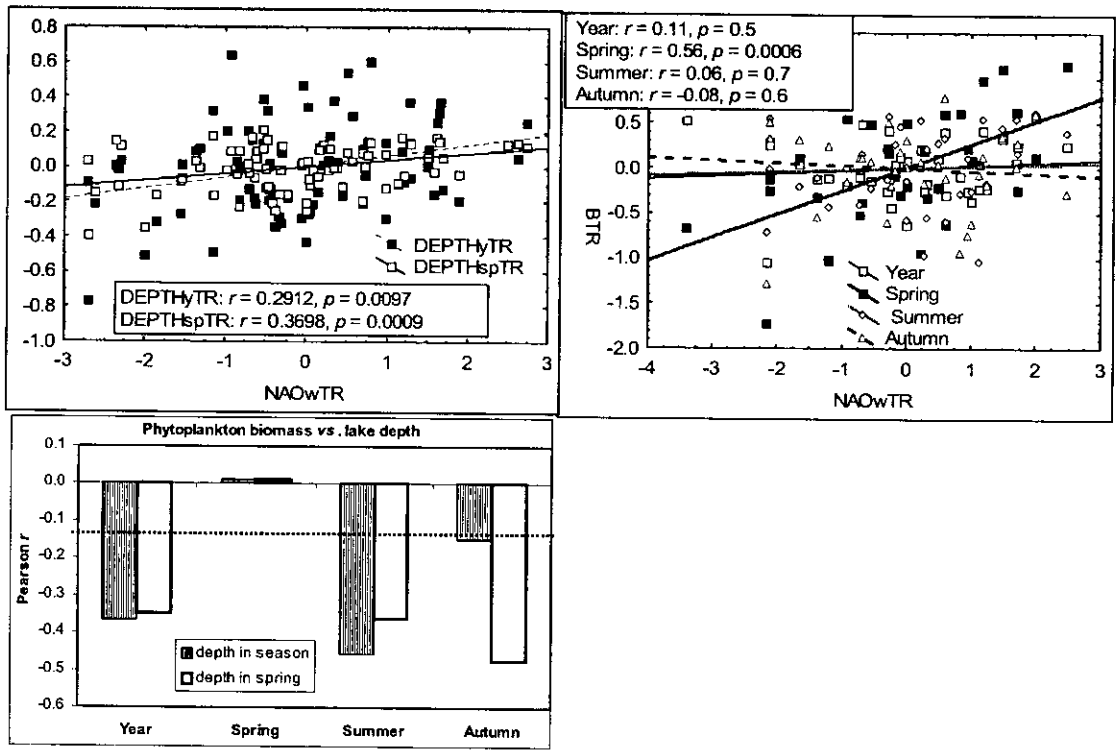

Fig. 20 Correlation of the transformed and detrended time series of annual average and spring (March--May) depth of L. Võrtsjärv (DEPTHyTR and DEPTHspTr, respectively), and phytoplankton biomass (BTR) with the North Atlantic Oscillation Index in winter (NAOwTR), and the relation of phytoplankton biomass with lake depth in different seasons (Nõges, submitted).

Weaker resuspension in deeper water releases less phosphorus from the bottom sediments while lower denitrification rate keeps nitrogen concentration high (Fig. 21). Consequently, in a warmer world the N/P ratio in Lake Võrtsjärv would probably be higher and potentially toxic N_2-fixing

cyanobacteria (blue-green algae) will have less chance to develop (Fig. 22), thus the risk of toxic water blooms will be reduced.

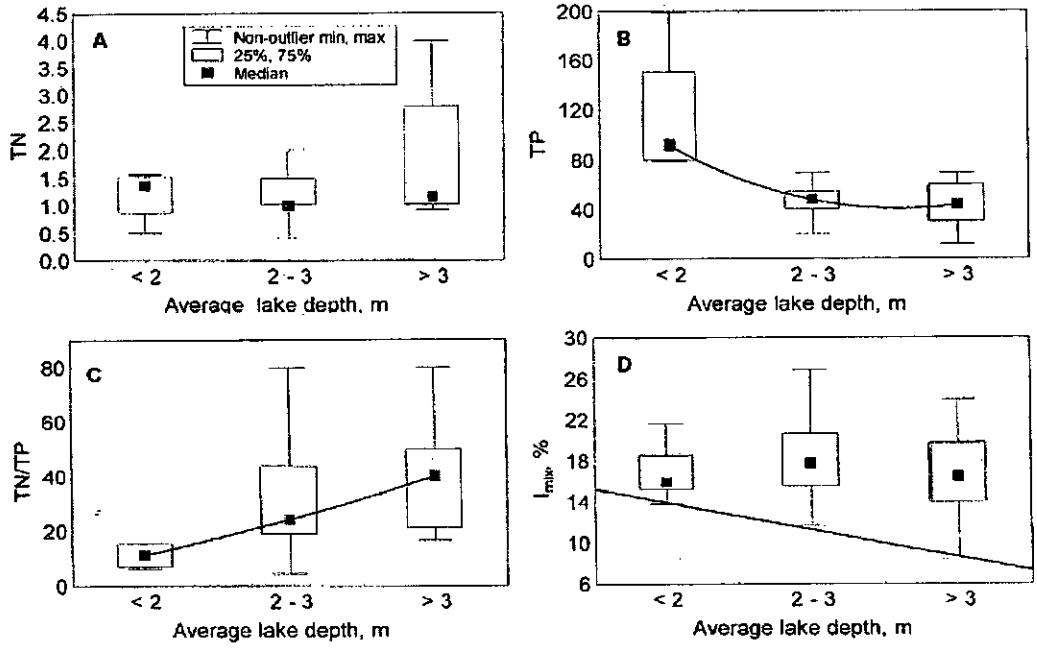

Fig. 21 Relationship between the mean depth and concentration of total nitrogen (TN), total phosphorus (TP), TN/TP mass ratio and average irradiance of the water column I_{mix}% in L. Võrtsjärv (Nõges et al. 2003b).

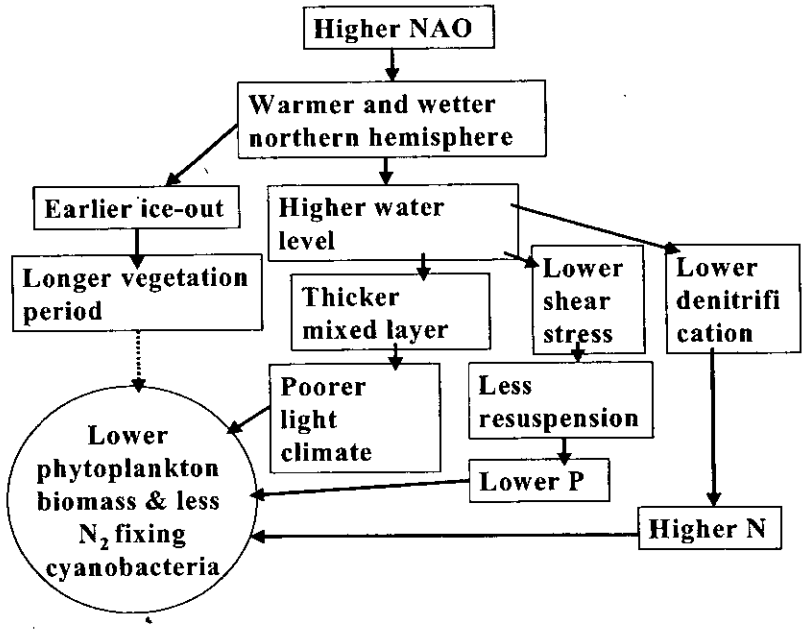

Fig. 22 Consequences of global warming on phytoplankton in Lake Võrtsjärv (Nõges et al., 2003a).

2.9 Lakes Vänern, Mälaren and Erken, Sweden

The total phytoplankton biomass was studied at 11 lake sites in the Swedish lakes Vänern, Vättern, Mälaren and Erken. Long-term changes have been observed for a shift in the maximum spring phytoplankton biomass that nowadays, as especially winter air temperatures become warmer, occurs earlier in the year (Weyhenmeyer et al. 1999). In general, chlorophyll *a* concentrations tend to be much higher below the ice cover during warm winters when there is no snow on the ice (Pettersson et al. 2003). Comparing a warm winter period (1989 to 1995) with a cold winter period (1982 to 1988) the phytoplankton spring bloom occurred about one month earlier after warm winters in Sweden's largest lakes Vänern, Vättern and Mälaren (Weyhenmeyer 2001). This implies an extension of the phytoplankton growing season. Significant changes in the mean total phytoplankton biomass during the icefree season from May to October could, however, not be observed as winter air temperatures became warmer. The total phytoplankton biomass was also not affected when comparing years with an ice cover with years without an ice cover in Sweden's largest lakes Vänern and Vättern (Westöö 2004).

In Lake Erken the shift in the spring phytoplankton biomass peak could be related to both, regional climatic atmospheric circulation (Blenckner and Chen 2003) and the large scale climatic process North Atlantic Oscillation (NAO) (Weyhenmeyer et al. 1999). This shift caused higher chlorophyll *a* concentrations early in the year, as seen by positive relationships between the NAO and chlorophyll *a* concentrations in March and April in Sweden's largest lakes Vänern, Vättern and Mälaren (Fig. 24 and Weyhenmeyer 2004). An earlier phytoplankton spring peak caused also an earlier population decline of the phytoplankton, as seen by negative relationships between the NAO and chlorophyll *a* concentrations in May (Fig. 24). During summer no significant relationships between the NAO and chlorophyll *a* concentrations could be observed in the large lakes Vänern, Vättern and Mälaren. In the relatively shallow Lake Erken, however, summer phytoplankton biomass was higher during warm years with a high NAO, probably due to increased mineralization rates by enhanced bacterial activity in the warmer waters.

First in autumn, the NAO was again related to chlorophyll *a* concentrations in the deepest Lake Vättern (Fig. 24). At this time also water temperatures were related to the NAO. The relationships result from the fact that the strong NAO signal on water temperature in May was

stored in the hypolimnion during summer stratification and became apparent again at the water surface in autumn when the water column was mixed. This implies that higher spring water temperatures might be the reason for higher autumn surface water temperatures in deep stratified lakes that favors the phytoplankton growth in autumn.

Not only ice cover and temperature had an effect on the phytoplankton biomass, but also an extreme precipitation event that caused unusual high biomass values in the Swedish Lake Mälaren (Weyhenmeyer et al. 2004).

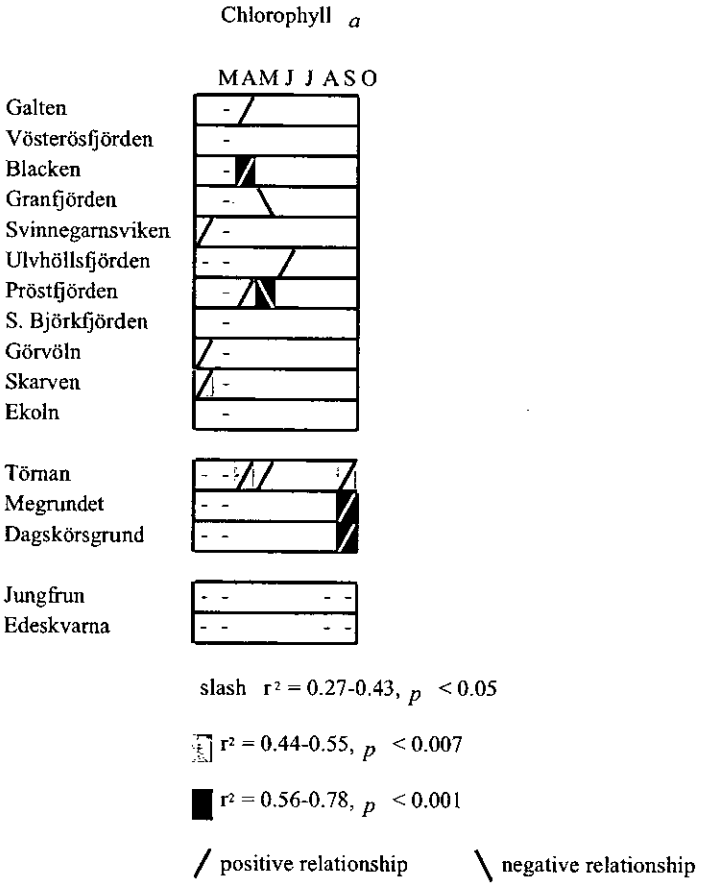

Fig. 23 Linear regressions of the North Atlantic Oscillation winter index on chlorophyll a concentrations in surface waters at 16 lake sites in the lakes Mälaren, Vänern and Vättern in the period March to October from 1981 to 1995. Grey and black boxes indicate that regressions remain significant after a correction of the p-value (the p-value was corrected for the number of regressions that have been carried out for each water chemical variable at each lake site, i.e. seven regressions), empty boxes reflect non-significant regressions ($p > 0.05$) and short lines are a symbol for missing data.

2.10 Lakes Pääjärvi and Valkea-Kotinen, Finland

Annual variations in summer phytoplankton biomass (June-August) in relation to winter NAO index, local variations in the weather and to physical and chemical properties were studied in the Finnish primary and secondary lakes, Pääjärvi and Valkea-Kotinen, respectively. In the oligo-mesotrophic and brown-watered Lake Pääjärvi phytoplankton data consisted of monthly samples for the summer period 1982-2003. For the small and humic Lake Valkea-Kotinen the data included weekly phytoplankton total biomass (as chlorophyll) for the open water period from 13 years (1990-2002).

In Lake Pääjärvi, phytoplankton biomass in the epilimnion (0-15 m) averaged 0.98 g m^{-3} (wet weight) (min-max: 0.32-3.19 g m^{-3}) in June-August during the 22-yr study period. The most abundant algal groups were cryptomonads and diatoms contributing together 30-95 % (mean 65%) of the total phytoplankton biomass during summer. The role of cyanobacteria (blue-green algae) in the total algal biomass was generally small throughout the study period. There was a decreasing trend in the total phytoplankton biomass during the study period, and on a monthly basis this was most evident in June. After log(x+1) transformation and detrending, the total phytoplankton biomass in June correlated negatively with the winter NAO index ($r=-0.43$, $n=22$). Similar relationship was found between the NAOwin and the biomass of diatoms in June ($r=-0.44$, $n=22$). On the contrary, higher winter NAO was related to higher cyanobacterial abundance in June ($r=0.46$, $n=22$). The reason behind the winter NAO impact on June phytoplankton abundance likely lies on the earlier ice-break-up during the high NAO years. This would mean that during the years with earlier ice break-up spring/early summer diatoms peak earlier and their abundance is already decreasing during the June phytoplankton sampling. The increased cyanobacterial abundance in June might be related to higher water temperature, although there was no relationship between the epilimnetic temperature and cyanobacterial biomass in June.

In Lake Valkea-Kotinen, phytoplankton biomass is dominated by flagellates, especially the raphidophyte *Gonyostomum semen*. Year-to-year variations in summer algal biomass (expressed as chl-a concentration) in the epilimnion (0-2 m) are large in the lake; individual measurements ranging from 4.5 to 187 mg chl-a m^{-3} (mean 38 mg chl-a m^{-3}). During the years 1990-2002, there was a decreasing trend in the epilimnetic chlorophyll concentration, which can largely be

explained by the very high abundance of *Gonyostomum* in the early 1990's in the lake. After detrending, the variations in epilimnetic chlorophyll during the summer months could not be clearly related to winter NAO index or regional weather conditions. In May, there was a negative correlation between the epilimnetic chlorophyll and winter NAO (r=-0.58, n=12), but this relationship was mainly based on two data points.

3 Comparative analyses

Standardized seasonal courses of phytoplankton biomass were calculated for 15 study lakes within the three lake regions, i.e., Northern lakes (including Lakes Võrtsjärv and Müggelsee), Western lakes, and perialpine lakes (Fig. 25). Standardized values were based on time series of either chl a concentrations (Esthwaite Water, Lakes Erken, Windermere, Lough Leane, and Mondsee) or on total phytoplankton biovolume (all other lakes). With the exception of Lake Erken no complete seasonal cycles can be shown for the Scandinavian lakes and basins, as no measurements under the ice were performed.

The lakes clearly show differences in mean growth patterns. Most notably, some lakes do show unimodal average growth patterns with a summer/autumn peak of phytoplankton, whereas in other lakes phytoplankton shows spring and summer blooms, with a clear drop in average biomass in-between, usually around May and June. Both, unimodal and bimodal growth patterns occur in all three regions studied. For example, bimodal growth pattern occur in Lakes Erken and Müggelsee (Northern Lakes), Esthwaite Water and Lake Windermere (Western Lakes) and in Lakes Constance, Greifensee, Mondsee and Zurich (Perialpine Lakes). In most cases, expression of one or the other seasonal growth pattern is due to the trophic status of a lake, with oligotrophic lakes exhibiting unimodal and mesotrophic/eutrophic lakes exhibiting bimodal growth patterns (Sommer, Gliwicz, Lampert, and Duncan 1986). Hence, lakes may shift with changes in trophic status from e.g. bimodal to unimodal growth patterns (see chapter 2.2). On average, the seasonal biomass maximum occurs in some of the bimodal lakes during spring (e.g., in Lakes Erken, Greifen and Mondsee), in summer (Esthwaite Water), or spring and summer peaks are of a similar magnitude. In lakes with a unimodal growth pattern, the annual peak usually occurs in summer, but might be postponed until September/October, for example in Lake Võrtsjärv.

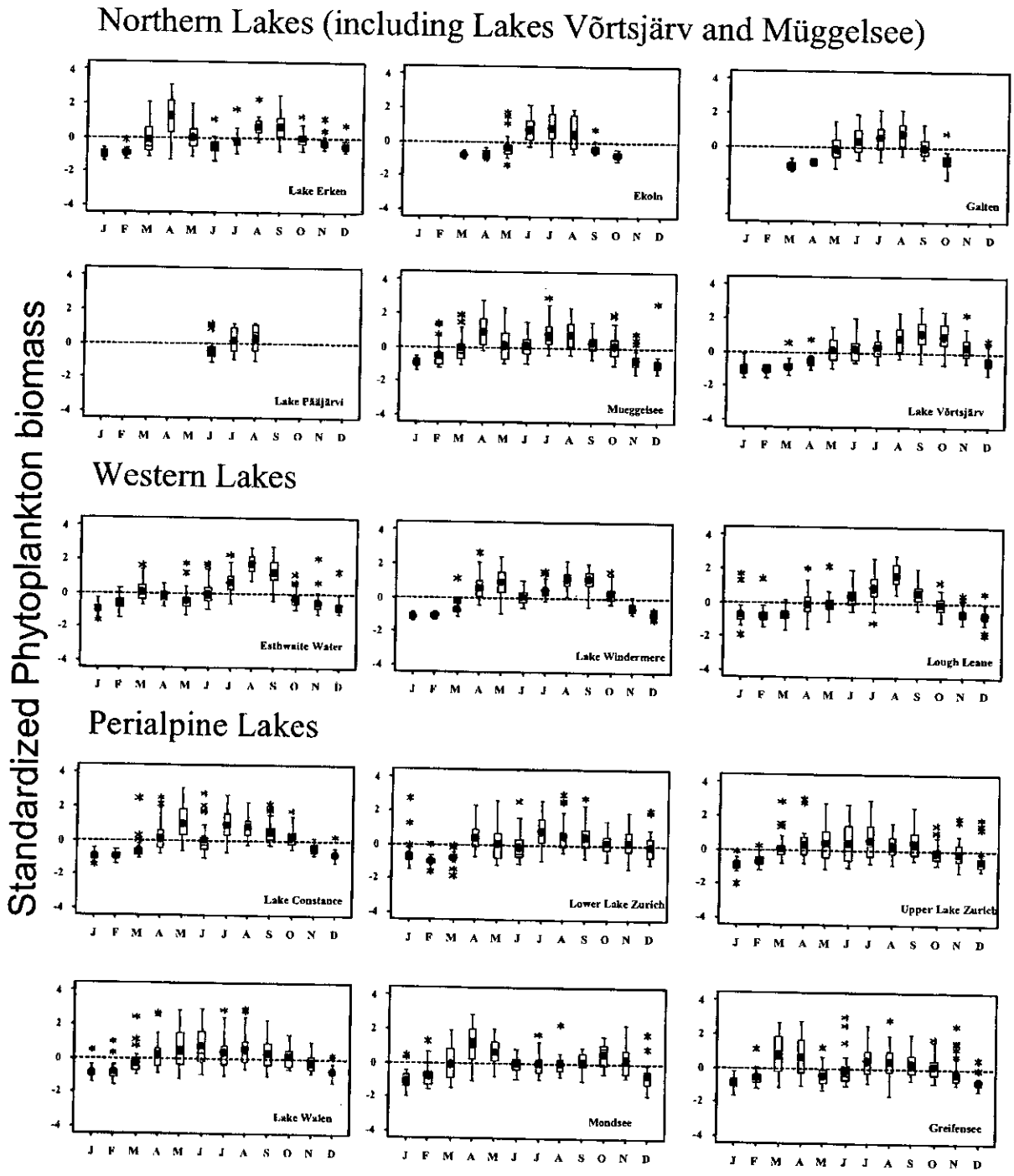

Fig. 25 Box plots of standardized phytoplankton biomass in the CLIME lakes. Stars represent individual measurements classified as outliers, i.e. deviating more than 1.5 standard deviations from the monthly medians of standardized values.

To analyze the influence of climate variability on growth pattern we study the influence of the North Atlantic Oscillation on biomass variability of phytoplankton. The NAO oscillation has been shown to influence the lakes in all three regions studied (this report, and for example (Weyhenmeyer, Blenckner, and Pettersson 1999;Straile 2002;George, Maberly, and Hewitt 2004)). As many lakes were influenced in addition to climate variability by changes in nutrient loads, i.e., eutrophication and oligotrophication, we used loess fits to remove temporal trends from the time series. The loess fits were chosen based on Akaikes information criteria. Phytoplankton data since 1975 were included into the analysis.

Fig. 26 shows the seasonal course of correlation coefficients of detrended phytoplankton biomass (chla) concentrations with the NAO winter index for Northern, Western and perialpine lakes. Significant correlation of phytoplankton biomass with the NAO, i.e. influences of climate variability on phytoplankton growth patterns, are neither restricted to a specific region nor to a specific season.

Surprisingly, a significantly positive correlation during spring was found only in Lake Võrtsjärv, although positive correlations of phytoplankton biomass have been reported for CLIME lakes during spring in other studies (e.g. (Weyhenmeyer, Blenckner, and Pettersson 1999;e.g., Straile and Adrian 2000;Gerten and Adrian 2000) and chapter 2.9) using other statistical methods and time windows. These relationships between spring phytoplankton biomass and the NAO are mostly mediated via the effect of the NAO on the timing of ice break-off. Consequently, a similar relationship is not expected for the Western and most large perialpine lakes which do not or only hardly freeze.

A number of significant correlations (positive and negative) were observed during summer and autumn, i.e. during a time period where no direct influence of the NAO can be expected. However, it has been shown that e.g. food web interactions can postpone NAO effects into the summer (Straile, Livingstone, Weyhenmeyer, and George 2003). This suggests that we have to be aware of complex mechanisms relating clime variability to phytoplankton biomass in European lakes.

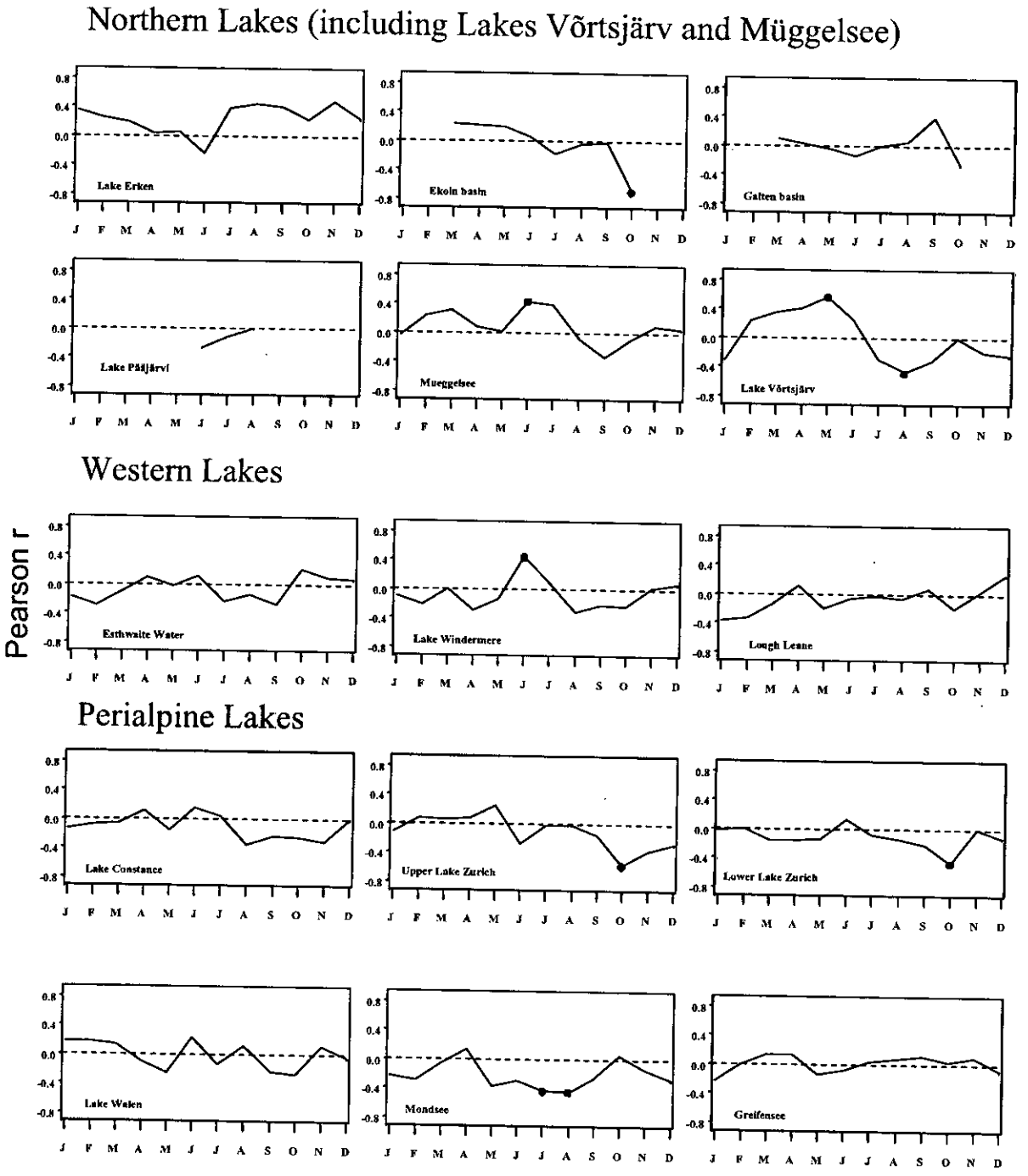

Fig. 26 Seasonal courses of correlation coefficients between detrended monthly values of phytoplankton biomass or chlorophyll and the NAO winter index. Dots indicate correlation coefficients significant at $p < 0.05$. Note that the significantly negative correlations observed during summer in Mondsee are largely due to one year, 1996. 1996 is the year with the most negative NAO index during the study years and a exceptionally high chl a concentration in Mondsee during summer.

Clearly, these results have to be interpreted with care, as by doing a large number of correlations and by choosing an alpha error of 0.05; we expect 5 % of all correlations to be significant by chance alone. The number of significant correlations observed in Fig. 26 (n=9) is hence hardly above the number of correlations expected by chance alone. However, a number of reasons suggest that these significant relationships indeed suggest an influence of climate variability on phytoplankton growth patterns in the study lakes:

1) the methods chosen for this comparative study did not detect all significant relationships observed by studies concerning individual lakes, which analyses were specifically tailored to the relevant data. For example, no significant relationships between the NAO and summer chl a concentration in Lake Erken were observed in this comparative study. However, Pettersen et al (2003) show that there is a clear difference in summer chl a concentrations after years with a cold as compared to a year with a warm winter.

2) as for many lakes the temporal resolution is one per month, we might have missed some of the the more subtle and short lasting effects of climate variability (see chapter 2.1)

3) the mechanisms for many of the reported significant relationships were studied and understood in some detail (see this report) and hence it can be excluded that the observed relationships are to a large extent spurious.

4 Summary

This report presents clear evidence for a European wide influence of climate variability on phytoplankton growth patterns. It revealed a multitude of mechanisms (e.g., via influences on the timing of ice-off, flushing, water levels, nutrients, grazing) on how phytoplankton growth patterns might be more or less directly be influenced by climate variability. The multitude of mechanisms can result into time lags between the timing of the meteorological forcing, i.e. during winter/early spring in the case of the NAO, and its effects on phytoplankton. Also, due to the multitude of mechanisms and due to the possibility of time lags one single climate signal such as the North Atlantic Oscillation can influence phytoplankton growth positively as well as negatively even within one lake during different parts of the season. Likewise, during one season phytoplankton can be positively related to climate variability in one lake and negatively in another one. For example, there is evidence that summer chla in Lake Erken is positively related to winter climate variability, whereas e.g., in Lake Võrtsjärv phytoplankton is negatively related

to the NAO in summer.

With our comparative analysis we did not observe clear region-specific impacts of climate variability on phytoplankton growth patterns, with the exception that spring, ice-off mediated effects of the NAO are more prevalent in the Northern lakes. Rather, phytoplankton in lakes will react differently based on their morphology, geographic setting and possibly also trophic status. This warrants further studies examining the detailed mechanisms relating phytoplankton growth pattern to climate variability.

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